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BIOLOGY OF THE ATLANTIC MACKEREL (*Scomber scombrus*) OF NORTH AMERICA

Part I: Early life history, including the growth, drift, and mortality of the egg and larval populations

By OSCAR ELTON SETTE

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ABSTRACT

This portion of a comprehensive study on the Atlantic mackerel (*Scomber scombrus*) treats of the early life history from spawning up to about the time the schooling habit develops, with emphasis on the quantitative aspects.

Spawning takes place along the Atlantic coast, mostly 10 to 30 miles from shore, from Chesapeake Bay to Newfoundland, with perhaps $\frac{9}{10}$ of the volume between the Chesapeake Capes and Cape Cod; $\frac{1}{10}$ in the southern half of the Gulf of St. Lawrence, and negligible amounts elsewhere. Embryological development at the temperature usually encountered occupies about 1 week. The pelagic eggs are confined to a surface stratum 15–25 meters thick. Hatching at 3 mm. of length, larvae grow to 10 mm. in about 26 days, and to 50 mm. in an additional 40 days, by which length they approximate the typical form for adult mackerel, and assume the schooling habit.

In 1932, it is estimated, 64,000 billion eggs were produced south of Cape Cod by a spawning population estimated at 100 million individuals. That year dominant northeasterly winds (which were abnormally strong) drifted one concentration of larvae, originating off northern New Jersey, and another concentration, originating off southern New Jersey, in a southwesterly direction, to localities abreast of Delaware Bay and Chesapeake Capes, respectively. A reversal of dominant winds, consequently of drift, returned both groups to northern New Jersey, by the 9-mm. stage of growth.

Mortality during most of the developmental period was 10 to 14 percent per day, but was as high as 30 to 45 percent per day during the 8- to 10-millimeter period when fin development was rapid. Survival from spawning of the eggs to the end of the planktonic phase of life (50 mm.) was in the order of 1 to 10 fish per million eggs spawned. This rate of survival is an abnormally low one since the fish from this spawning season were abnormally scarce in the adult populations of subsequent years. The low survival rate is ascribed to the abnormal amount of southerly drift, coupled with a general scarcity of plankton in the spring of 1932.

BIOLOGY OF THE ATLANTIC MACKEREL *(SCOMBER SCOMBRUS)* OF NORTH AMERICA. PART 1: EARLY LIFE HISTORY, INCLUDING GROWTH, DRIFT, AND MORTALITY OF THE EGG AND LARVAL POPULATIONS

By OSCAR ELTON SETTE, *United States Fish and Wildlife Service*

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INTRODUCTION

The common mackerel, *Scomber scombrus*, is found on both sides of the Atlantic Ocean, approximately between the 30th and 50th parallels of north latitude. Although American and European representatives are very much alike in appearance, life history, and habits, their ranges are discontinuous, so that the two populations may be regarded as separate races with no intermigration. Consistent with this view is the observation (Garstang, 1898, p. 284) that the two stocks differ in morphological characters.

The American race has from colonial times been caught and marketed in large volume.[1] In the nineteenth century the annual yield occasionally reached 200,000,000 pounds. The present yield is about 60,000,000 to 80,000,000 pounds annually, of which the United States fishery takes about three-quarters and the Canadian fishery the remainder (Sette and Needler, 1934, p. 43).

[1] The European race, too, is the object of an important commercial fishery, but appears never to have been held as high in esteem or occupied so high a rank among the commercial fishes of Europe as has its American relative among the fishes of this side of the Atlantic. Fishery Bulletin 38. Approved for publication May 15, 1939.

Among the commercial fishes, the mackerel is remarkable for its spectacular changes in yield. To illustrate this, only a few records need be selected (Sette and Needler, 1934, p. 25). From 116,000,000 pounds in 1834 the United States catch dropped to 23,000,000 pounds in 1840, only to rise again to 137,000,000 pounds in 1848. From its peak of 179,000,000 in 1884, the catch dropped to 30,000,000 in 1886, only 2 years later. More recently it increased from 13,000,000 pounds in 1922 to 68,000,000 pounds in 1926. For the United States and Canada together the largest catch, 234,000,000 pounds, was landed in 1884, the lowest, 12,600,000 pounds in 1910.

Although these fluctuations had profound effects both on the economic welfare of the fishermen and on the business of the fish markets, and although speculation, both popular and scientific, as to the causes of these sharp changes in returns from the fishery, has been indulged in for many years, no satisfying explanation has been forthcoming. This is not particularly surprising, for the scientific research concerning work on this species has been of desultory nature and unsuited to the solution of a problem as intricate as is presented by the fluctuations in fish populations. Nonetheless, from the fragmentary records then available, Bigelow and Welsh (1925, pp. 198–199) found evidence suggesting that the mackerel, like the Norwegian herring, was subject to marked inequalities in the annual success of reproduction or of survival to commercial size of the various year classes, and attributed the intermittently good and poor years of fishing to intermittently good and poor seasons of spawning or survival.

This hypothesis, being the most reasonable one thus far advanced, determined the method of approach in the present investigation. Obviously, its pursuit required two basic series of observations: (1) An estimate of changes in abundance, and (2) determination of changes in age composition. Carried through a number of years, these observations should provide material for measuring the relative numerical strengths of year classes arising from each season's spawning, for tracing the influence of the annual increments afforded by each year class and their subsequent mortality on the success of the commercial fishery, and conversely for examining the influence of the commercial fishery both on the reproductive success and on the mortality.

Accordingly, after some preliminary field work in 1925 at Woods Hole and Boston, Mass., in which various techniques of sampling and measuring were developed, a routine program of observations was commenced at the principal mackerel fishing ports. For the estimation of changes in abundance, pertinent details covering the landings by mackerel vessels were recorded to form the basis for computing catch per unit of fishing effort; and for the determination of age-composition, samples of mackerel were drawn daily from each of a number of the fares landed. These basic observations began in 1926 and have continued to the present time. In addition, inquiries were pursued into the natural history and habits of the mackerel, since more adequate knowledge of these was required for interpretation of the data derived from the commercial fishery.

During the 10 years, 1926 to 1935, sufficient material has accumulated to provide substantial contributions to the understanding of the life history of the mackerel, with special reference to its fluctuations in abundance; and, accordingly, a series of papers, of which this is the first, is to be published.[2] The present paper deals with features of the early life history, with particular reference to the understanding of variations in the annual replenishment of the commercial stock. It summarizes present knowledge

[2] Results, of preliminary nature, previously published are to be found in Sette, 1931, 1932, 1933, and 1934. Also see Sette and Needler, 1934.

of the course of events from the time the eggs are spawned until the young mackerel attain the juvenile phase and closely resemble the adults in form and habits. Other papers in this series, now in course of preparation, deal with (1) habits and migrations, (2) age and rate of growth, and (3) fluctuations in abundance of the commercial stock.

Acknowledgments.—The entire portion of the mackerel's life considered in this paper is passed suspended in the waters of the sea, hence as a member of the plankton community. Accordingly, the data were secured by towing fine-meshed plankton nets through the waters of the spawning grounds. A preliminary cruise in Massachusetts Bay was taken in 1926 on the U. S. Fisheries steamer *Gannet*, Captain Greenleaf, commanding. Cruises in succeeding seasons 1927 to 1932 were on the U. S. Fisheries research steamer *Albatross II*, Captain Carlson, commanding. In June 1932 the *Albatross II* was taken out of service and completion of that season's program was made possible by the kindness of the Woods Hole Oceanographic Institution in putting at our disposal for two cruises during June and July the ketch *Atlantis*, Captain MacMurray, commanding.

Numerous persons assisted in the scientific work aboard ship. Of these, E. W. Bailey, Wm. C. Neville, and Herbert Ingersoll took part in many cruises. Wm. C. Herrington's suggestions contributed greatly to the development of the use of current meters to measure flow through the plankton nets.

In the separation of eggs and larvae from the other planktonts, numerous persons assisted, but the major portion of the responsibility rested on Mildred Moses, whose vigilance insured a constant level of accuracy in removal of the desired material. Her performance of subsequent numerical computations was also an important contribution to the present results.

To C. P. Winsor I am indebted for suggestions relating to the statistical treatment of the mortality curves.

Certain tabulations and the graphs used herein were products of W. P. A. official project No. 165-14-6999.

Throughout the investigation, and in all of its many phases, the constantly available encouragement and advice of Henry B. Bigelow has been invaluable. To the extent that this account proves readable, the reader may thank Lionel A. Walford whose editorial suggestions have been freely followed.

ACCOUNT OF FIELD WORK

As before mentioned, when work began in 1925 it was strongly suspected that the fluctuations were due mainly to annual variations in the comparative success of survival through the larval stages (Bigelow and Welsh, 1925, pp. 198–199). Accordingly, work on the early life history was begun at the outset of the investigation in 1926. At that time, it was not known where most of the spawning took place or where the nursery grounds for larvae were located. The literature recorded the occasional finding of eggs in the sea south of the Gulf of St. Lawrence, but no larvae; yet the spawning population apparently favored the southerly waters off the United States coast as much as the northerly waters off the Canadian coast. Massachusetts Bay was a spring mackerel fishing ground well known to be visited at this season by numerous ripe adult individuals, so the first search took place there. Towing in various parts of the bay yielded large numbers of eggs, especially in that portion of the waters partially enclosed by Cape Cod. Not only were the eggs abundant, but numbers of larvae in various stages of development were found.

Encouraged by this success in waters south of the previously known distribution of larvae, search was in 1927 extended south of Cape Cod. Here eggs were found in abundance from the offing of Cape Cod nearly to the mouth of Chesapeake Bay. As in Massachusetts Bay, larvae were present in abundance also.

To determine whether this was the usual condition, the survey was repeated in a single cruise during May of 1928, when approximately the same conditions were found.

These three seasons of prospecting for mackerel eggs and larvae completely altered the previous notion that spawning was more successful in the northwest portions of the range of the species. Not only were specimens regularly obtained from Massachusetts Bay to Chesapeake Bay, but the numbers of individuals per tow were greatly in excess of those taken by similar methods in the Gulf of St. Lawrence during the Canadian Fisheries expedition of 1914–15. Evidently this southerly region was far more important than previously supposed, and hence a suitable one in which to study variations in the survival rate during early stages.

However, it was still necessary to determine the length of the spawning season and the duration of the period of larval development. For this purpose, successive cruises were made during the spring and early summer months of 1929. These proved that in the area between Cape Cod and Cape Hatteras spawning began in early April, and larval development had nearly run its course by the end of July.

In 1930 and 1931, such successive cruises during the spawning season were repeated and every opportunity was taken to devise methods of estimating the abundance of the various young stages.

This development of quantitative technique required the determination of vertical distribution so that the proper levels would be fished; determination of the incubation and growth rates so that cruises might be planned at proper intervals to include all the important events; and finally, it required devising a reliable method of measuring the amount of water strained by the tow nets so that hauls would be comparable from time to time and place to place. By 1932 knowledge and techniques were advanced sufficiently for the survey of that season to provide adequately quantitative data for the more important sections of this report dealing with growth, drift, and mortality. Toward the close of this season, the *Albatross II* was withdrawn from service as a Government economy measure. This prevented continuing the research into its next phase, that is, the measurement of mortality and its accompanying hydrobiological conditions through a series of seasons, to see how mortality is affected by particular conditions in seasons of good survival contrasted with other conditions in seasons of poor survival. Since the hoped-for resumption of surveys has not yet been possible, the present available results are now reported.

SYNOPSIS OF RESULTS

Most mackerel reach reproductive maturity when 2 years old. Some precocious individuals, usually males, first spawn a season earlier and others of both sexes a year later. The percentage of the latter is higher among the females than the males.

Mackerel are said to spawn 360,000 to 450,000 eggs in a season, but this is a point needing further study. Doubtless smaller individuals spawn fewer and larger individuals more eggs than this. The eggs are ripened in successive batches; it is not known how many batches or what interval of time intervenes between their discharge.

Spawning takes place over nearly the entire spring and summer range of the species, from off Chesapeake Bay to Newfoundland. By far the most important ground is between the Chesapeake capes and Cape Cod; second in importance, with perhaps one-tenth as much spawning, is the southern half of the Gulf of St. Lawrence. Other stretches of the coastal waters may at times receive negligible amounts of spawn, but it is safe to say that the entire Gulf of Maine (excepting Cape Cod Bay), and the entire outer coast of Nova Scotia, the northern two-thirds of the Gulf of St. Lawrence and the waters around Newfoundland are not regular spawning grounds of any importance.

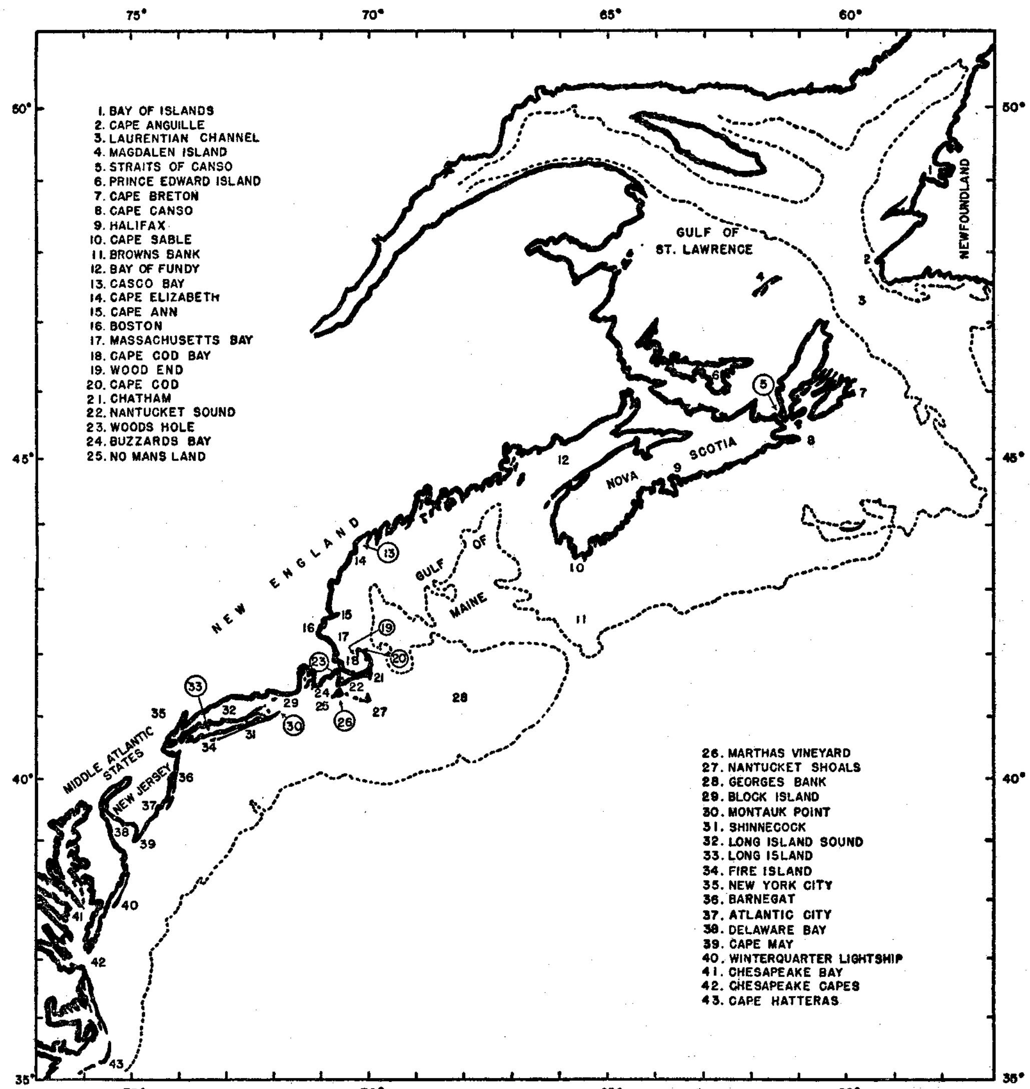

FIGURE 1.—Geographical features and landmarks mentioned in the text.

Spawning takes place in open waters in some places close to shore, in others as far as 80 miles to sea, but mostly 10 to 30 miles from shore. Open bays, such as Cape Cod Bay and Casco Bay, are spawning sites of minor importance while well-enclosed bays and sounds, especially those receiving considerable river water, such as Chesapeake Bay, Delaware Bay, and Long Island Sound, are neglected by the spawning mackerel.

Spawning occurs at any time of day or night, and probably near surface.

Embryological development is similar to that of other teleost fishes. It progresses more rapidly in warm water than in cold, eggs hatching in 2 days at 21° C. (70° F.) and in 8½ days at 10° C. (50° F.). The prevailing temperatures on the spawning grounds at the height of the spawning season are between 9° and 12° C., so that in nature the incubation period usually occupies about a week.

During incubation the eggs are suspended in the sea water between its surface and the thermocline, which is usually 15 to 25 meters (8 to 13 fathoms) deep in the area studied. They have a tendency to sink gradually as development proceeds, so that the late stages are found at deeper levels than the early ones, but even so, not below the thermocline.

After hatching, the young mackerel passes through three phases of development, conveniently designated as yolk sac, larval, and post-larval stages. During the yolk sac stage—a matter of about 5 days—the fish is about 3 mm. (⅛-inch) long and subsists on the yolk. During this period, the mouth and digestive organs develop into usefulness and the yolk sac is absorbed. During the period occupied by the larval stage, that is, between yolk sac absorption and development of fins, which lasts about 26 days, the fish grows from a length of 4 mm. (⅙-inch) to 10 mm. (⅜-inch) in length. Then, when the fins have appeared, the post-larval stage begins. It continues about 40 days and during this time the fish grows to a length of about 50 mm. Toward the end of this stage, while growing from 30 to 50 mm., the body assumes the trim fusiform shape of the adult. At that time, the fins, relative to the body, are even larger than in the adult, and the coloration includes shiny, silvery iridescence, though still lacking the characteristic wavy black bands of the adult.

During the yolk sac stage, movements are feeble, not even serving to keep the fish right side up. Swimming faculties increase during the larval stage and are exercised in performing vertical diurnal migrations, the larvae ascending toward the surface at night and descending toward the thermocline at day. But they do not swim any considerable distances during this stage; instead they drift with the water masses in which they are suspended. In post-larval stages, true swimming takes place, the young fish at times moving in a direction opposite to the prevailing drift of water. The schooling habit probably begins to assert itself toward the end of this stage and thereafter is followed in much the same fashion as by the adults.

In 1932, the larvae were drifted initially in a southwesterly direction, and the main body was transported about 80 miles down the coast, one subgroup drifting from the offing of northern New Jersey to the offing of Delaware Bay; another, from the offing of southern New Jersey nearly to the Chesapeake capes. Then, a reversal of drift returned both groups to the offing of northern New Jersey by the time they had reached the end of the larval stage, and were 9 mm. long. The southwesterly drift coincided with the predominance of northeasterly winds, and the northeasterly return with a reversal of dominant winds.

Compared with other seasons, 1932 had an abnormally large northeasterly wind component, which left the 9-mm. larvae farther to the southwest and farther offshore than in other seasons. After the post-larval stage of active swimming commenced, the direction of travel was toward southern New England, and by the latter part of July, some of the largest of the post-larvae had even passed Nantucket Shoals and were taken off Cape Cod.

In 1932 the mortality over most of the developmental period was 10 to 14 percent per day. There was a notably higher mortality of 30 to 45 percent per day during the 8- to 10-mm. period, when fin development was rapid. Other departures from the general rate, of doubtful significance, were during egg stages, when about 5 percent per day was indicated, and during the yolk sac stage (3-mm. larvae), when about 23 percent per day was suffered.

The indicated total mortality, from the spawning of the eggs to the end of planktonic existence (50 mm. or 2 inches long), was 99.9996 percent. That is, the survival was in the order of magnitude of only 1 to 10 fish per 1,000,000 of newly spawned eggs.

This mortality was not due to sharply higher death rate at the yolk-sac stage—a theory of year-class failure holding favor among fishery biologists. Mortality was substantial in all stages. It was greatest during fin development in the transition phase from larval to post-larval stages. The higher mortality at this time appears to have been connected with the particular pattern of drift caused by the dominant wind movement, which in 1932 left the larvae farther than usual from their nursery grounds along the southern New England coast. This, together with a general scarcity of plankton, is considered the cause of failure of the 1932 year class.

SIGNIFICANCE OF RESULTS

Most conservationists lay particular stress on the maintenance of adequate spawning reserves. It is important to do so. If an annual commercial crop is to be constantly obtained, the spawning stock must be kept large enough to produce as many young as are needed to replace the fish caught by man and other predators. This can be done, in most cases, only by controlling the annual yield. From this springs an obvious, but not universally appreciated, fact that accumulating a surplus of spawners is a wasteful practice, for it means holding the annual yield below the amount that the resource is capable of producing. It would be simple, for instance, to insure an adequate spawning reserve by allowing no fish to be caught. But this would be more futile than to allow all to be caught. The latter would utilize one crop, the former none. Obviously, efficient exploitation calls for an intermediate course of action, one that would permit taking the maximum annual yield commensurate with the maintenance of an adequate spawning reserve; no more and no less.

But what is an adequate spawning reserve? It can be defined as one large enough to reproduce the young needed to recruit the commercial stock. Its determination is a matter of observing the numbers of recruits produced by spawning stocks of different sizes. Thus, the answer rests on knowledge of recruitment.

Two things affect recruitment: First, the numbers of spawners; second, the mortality in young stages—"infant mortality." The latter is tremendous and variable. Its variability is so great that it could readily obscure such correlation between number of spawners and number of recruits as might be present intrinsically. For example, under a given quality of survival conditions a large spawning population may produce a large number of recruits and a small population a small number of recruits, but with variable survival conditions a large number of spawners might produce only a small number of recruits if infant mortality be relatively high; and conversely, a small number of spawners might produce a large number of recruits if infant mortality be relatively low. As long as one can observe only the changes in numbers of spawners and numbers of recruits, the relation between the two cannot be seen, for it is obscured by the intervening infant mortality. Therefore, as long as the effect of infant mortality is unknown, so long will the size of an adequate spawning reserve be unknown.

Thus the measurement of infant mortality is the key to the problem. In the course of this study, a technique for making this measurement has been devised, and was applied during the season of 1932. With similar observations in enough additional seasons, it should be possible to determine what recruitment can be expected from given sizes of spawning stocks for particular infant mortality rates. Thus there will be determined an adequate spawning reserve, for it will be one that produces the needed average recruitment over the observed range of infant mortality rates.

LIFE HISTORY

REPRODUCTIVE AGE

According to information formerly available (Bigelow and Welsh, 1925, p. 205), "Some few females ripen when still not more than 11 inches long; most of them, and all males, at 12 to 13 inches." Present observations indicate first attainment of maturity at somewhat larger sizes, the difference possibly being due to the manner of measurement. The lengths given below were from snout to tip of the middle rays of the caudal fin, whereas the earlier measurements may have excluded the caudal fin.

Of 1,116 mackerel sampled from catches of traps in the vicinity of Woods Hole, Mass., and at three localities on the shores of Massachusetts Bay between June 24 and July 21, 1925, the smallest male with mature gonads was 26 cm. (10¼ inches) long and the smallest female 29.5 cm. (11⅝ inches). At 30.5 cm. (12 inches) 30 percent of the males and a negligible percentage of females were mature. At 34 cm. (13⅜ inches) about two-thirds of the males and one-half of the females were mature; and at 37 cm. (14⅝ inches) nine-tenths of both sexes were mature. (See fig. 2.)

It is possible that our data may not be typical because they were taken somewhat after the peak of spawning, which usually falls in May and June, and some individuals which had spawned early, and whose gonads had somewhat recovered, might have been mistaken for immature individuals. The number so mistaken cannot have been large for there was little difficulty in recognizing the two categories, "ripe" and "spent," which make up our class of "mature." The mistakes, if any, because the spawning of some individuals was too long past, should have been mostly among the larger sizes, because they are usually first to appear along the coast and presumably the earliest to spawn. But among these (52 specimens over 38 cm. in length were examined) only 1 individual appeared immature, hence the error, if any, must have been small.

By means of size and age relations to be published in another paper of this series, it may be concluded that only a few males, and even fewer females, spawn as yearlings. Four-fifths of the males and two-thirds of the females spawn when 2 years old, and virtually all of both sexes when 3 years old.

FECUNDITY

Various statements have appeared in the literature purporting to give the numbers of eggs spawned by individual mackerel. Brice (1898, p. 212) in "The Manual of Fish Culture" states that the average number of eggs at one stripping is about 40,000, that a 1½ pound fish gave 546,000, and that the largest fish yielded probably a full 1,000,000 eggs. Bigelow and Welsh (1925, p. 208) say, "Mackerel is a moderately prolific fish, females of medium size producing 360,000 to 450,000 eggs, but only a small part of these (40,000 to 50,000 on the average) are spawned at any one time." But Moore, whose report appears to be based on more intensive study than others, more cautiously states (J. P. Moore, 1899, p. 5) "seldom 50,000 and frequently a much lesser number of ova are produced at one time, but the aggregate number matured (in a spawning season) in one female of average size is several hundred thousand." This is probably as precise a statement as is warranted at the present time.

Moore (loc. cit.) has shown that there are successive batches of eggs ripened by an individual female during the course of the season. This introduces the uncertainty as to whether any particular enumeration has included, on the one hand, all batches destined to be spawned during the current season and, on the other hand, none that were destined to be spawned during a following season. The difficulty of making a correct decision is amply portrayed by the thorough study by Clark (1934) on the California sardine, *Sardinops caerulea*, a species which, like the mackerel, spawns successive batches. Clearly this subject requires additional study to provide statisti-

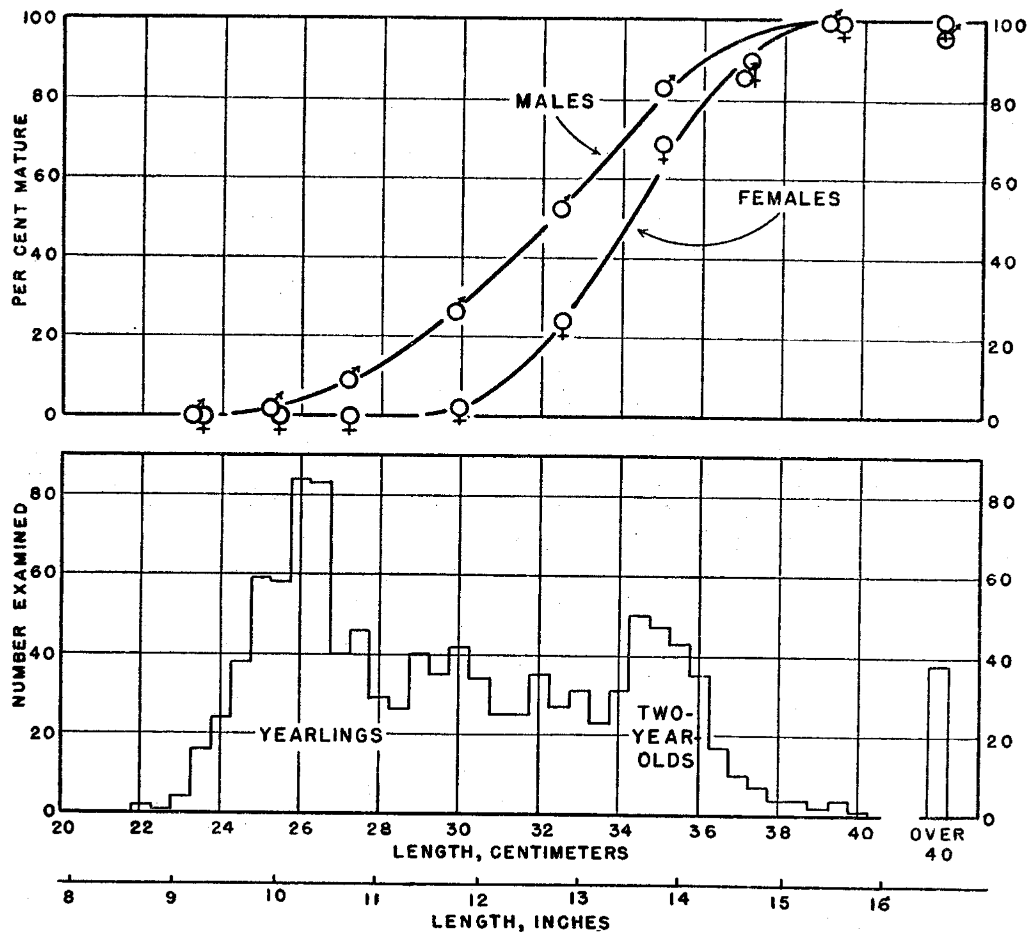

FIGURE 2.—Length and age at which mackerel reach reproductive maturity. The upper panel shows, by 2½ cm. length groups, the percentage of each sex matured. The lower part shows by half cm. length groups, the numbers examined for determination of percentage of maturity.

cally adequate data, and deserves such study because the ability to compute the number of eggs that can be produced by a population of known size-composition or, conversely, to compute the size of a parent population of known size-composition from the known numbers of eggs found in a spawning area would provide useful, if not indispensable, data for elucidating several perplexing problems connected with the fluctuations of fish populations and the management of fish resources. See pages 164 and 165 for an example of the uses of such data.

SPAWNING GROUNDS AND SPAWNING SEASONS

Bigelow and Welsh in 1925 (pp. 206–208) summarized the information available on the spawning of the mackerel. Apart from the generalization that mackerel spawn along the American Atlantic coast from Cape Hatteras to the Gulf of St. Lawrence mainly in spring and early summer, most of the conclusions reached at that time are now subject to revision. Their statement (p. 206) "* * * a much greater production of mackerel eggs takes place east and north than west and south of Cape Cod, with the Gulf of St. Lawrence far the most productive nursery for this fish," is particularly at variance with present available facts, as will appear from the following account of the numbers of mackerel eggs found in the various parts of the spawning range.

Coast of the Southern New England and Middle Atlantic States

Numbers and distribution.—Until the present investigations there was little known about the spawning in the great bight bordered by the shores of southern New England and the Middle Atlantic States. Although ripe individuals are commonly taken in the fishery in this area, no appraisal had been made of the egg concentrations to be found there; nor was it known whether larvae hatched from such eggs as were spawned there could survive; in fact it was suspected that reproduction was unsuccessful, for no larvae of the mackerel had been captured there.

As a result of information gained from the surveys of the present investigation during the seasons 1927–32, this region now appears to contain the most important spawning grounds of the mackerel. In horizontal tows at the surface, i. e., in the stratum of densest concentration, a meter net has taken, in 20 minutes, as many as 185,000 eggs. In 1929 the average catch per positive tow [3] of this kind was 2,600 eggs during the cruise of May 10 to 18, and 5,000 eggs during the cruise of May 28 to 31. These numbers may be taken as fairly typical of concentrations at the surface when and where spawning is active, and will be useful for comparison with other regions where similar data are available. More informative, in the absolute sense, are the results of oblique tows of 1932, which sampled all levels and covered systematically the entire region between Cape Cod and the Chesapeake Capes. The average catch of such tows, including all between May 2 and June 21, i. e., the major portion of the spawning season, and including both positive and negative tows, was slightly over 1,100 eggs. Since these tows strained 17 cubic meters of water per meter of depth fished, the average concentration was 65 eggs per square meter of sea surface.

Within this region eggs have been consistently most abundant along the inner portions of the continental shelf. The area of densest distribution occupies about the inner half of the shelf off New York with the zone narrowing and trending somewhat offshore southerly, and also narrowing but trending inshore northeasterly. By far the greatest concentrations have been found regularly somewhat southerly of the Fire Island Lightship, and this undoubtedly marks the usual center of greatest spawning activity.

So far as is now known, no spawning takes place in the enclosed waters of the bays and sounds west and south of Block Island. A few eggs are spawned in the southern part of Buzzards Bay and Vineyard Sound, but these are negligible in quantity compared with the spawning in open waters.

[3] Positive here indicates a tow in which mackerel eggs were caught.

Season.—Spawning begins in the southern end of this region during the middle of April about as soon as the mackerel appear in the offing of Chesapeake Bay. Thence it proceeds northeastward along the coast, taking place during the month of May off the New Jersey and New York coasts and extending into June off southern Massachusetts. In 1932, spawning in this region reached its climax about the middle of May. (See table 5.) Surveys of other spawning seasons indicate that this is the usual time of maximum spawning.

Temperature at spawning.—In this region we have found mackerel eggs in water as cool as 7.3° C. (45° F.) and as warm as 17.6° C. (64° F.). In 1932, the greatest numbers of eggs (98 percent) were found in water of 9.0° to 13.5° C. (48° to 57° F.) and this may be regarded as the range in which the bulk of mackerel eggs are usually spawned in this region.

Gulf of Maine

Numbers and distribution.—On visits to the western portions of the Gulf of Maine during the present investigation, eggs were found only in Cape Cod Bay. There the concentration was only slightly less than in waters south of Cape Cod but practically none were found in waters off the outer face of Cape Cod and the coast between Boston and Cape Elizabeth. Moore (1899) found them in the outer portions of Casco Bay in 1897, but the numbers were few. Bigelow and Welsh (1925, p. 206) occasionally found a few in various parts of the Gulf of Maine. The maximum haul was recorded by them as "200 plus."

Although Bigelow and Welsh (1925, p. 207) say, "That Nantucket Shoals, Georges Bank, and Browns Bank, like the Scotian banks to the east, are also the sites of a great production of mackerel eggs is proven by the ripe fish caught there * * * ", it now hardly appears likely that these banks around the periphery of the Gulf of Maine can be the site of important spawnings. The records of eggs taken by Bigelow and Welsh did not include any from these banks and during the present investigation the waters about Nantucket Shoals were visited repeatedly, and the western half of Georges Bank occasionally, without finding more than negligible numbers there. It is likely that the ripe fish caught on these grounds were a part of schools destined to spawn elsewhere, presumably the Gulf of St. Lawrence, and were taken during the course of migration to that area. This is in harmony with the results of investigations on migration which are to be reported on in another paper of this series.

Thus it appears that the only spawning ground regularly important in the Gulf of Maine is Cape Cod Bay. This body of water is so small compared with the grounds south of Cape Cod or with those of the Gulf of St. Lawrence that reproduction in the Gulf of Maine must be negligible compared with that of the other spawning regions.

Season.—Spawning probably takes place somewhat later in the Gulf of Maine than south of Cape Cod in consequence of later vernal warming and later incursion of mackerel into the waters of this region. It evidently was on the increase and perhaps near its maximum in Massachusetts Bay between June 9 and June 14 of 1926, when hauls taken on a line of three stations running out from Wood End Light toward the middle of Cape Cod Bay averaged 700 and 1,200 per tow on June 9 and 14, respectively. A more precise determination of the time of maximum spawning awaits the sorting of additional hauls made in 1926 and 1930.

Coast of Nova Scotia

Numbers and distribution.—Information on the occurrence of mackerel eggs along the coast of Nova Scotia is limited to the results of a survey in 1922 reported by Sparks (1929, pp. 443–452).[4] Stations were occupied along the entire coast from Cape Sable to the Straits of Canso during the period May 31 to September 18, but no eggs were taken after the middle of July. For the most part the hauls yielded very few eggs, the average number taken being 14 per station, which presumably represents the sum of three tows.[5] Although Sparks stated neither the dimensions of his nets nor the duration of his tows, it may be presumed that at least the surface net was a meter in diameter at the mouth and that the tows were 15 to 30 minutes in duration. If so, the egg concentration was exceedingly low compared with the other regions. Furthermore, the occurrence of eggs even in this low concentration was limited to a relatively narrow band along the coast (table 1). Thus the waters along the Nova Scotian coast are poorer in mackerel eggs than any others within the known habitat of the species.

Season.—Spawning occurs along the Nova Scotian coast from about the last of May to the middle of June.

TABLE 1.—*Number of mackerel eggs taken per station in Nova Scotian waters at various distances from shore*

Station	Distance	Number of eggs	Station	Distance	Number of eggs
	Miles			*Miles*	
380	1	2	381	7	14
384	2	6	386	9	0
383	6	19	382	11	6
385	6½	11			

Gulf of St. Lawrence

Numbers and distribution.—The Canadian Fisheries Expedition of 1914–15 explored the Gulf of St. Lawrence during the spring and summer of 1915 (Dannevig, 1919, pp. 8–12). Their surveys were made with a meter net hauled at the surface for 10 to 15 minutes, supplemented in many instances by vertical hauls, which, however, took few mackerel eggs. The average catch in horizontal tows was 324 eggs per positive haul, and the largest catch was 3,800 eggs. Since eggs were taken at almost all stations south of the 100-fathom contour marking the southern border of the Laurentian Channel, it may be presumed that mackerel spawn over this entire area. The numerous larvae taken there indicate that this area not only is the site of considerable spawning, but also that conditions there are suitable for the development of the larva. The largest larva taken measured 9 millimeters in length.

In addition to the catches in the southern part of the Gulf of St. Lawrence, a few larvae were taken near Cape Anguille on the southwestern coast of Newfoundland. Also, there was a number of mackerel eggs in a sample of fish eggs collected from the Bay of Islands by the Newfoundland Fishery Research Commission and referred to the Bureau of Fisheries for identification. It thus appears that spawning takes

[4] In addition to Sparks's results there is the listing by Dannevig (1919, p. 60) of two mackerel eggs taken off Halifax and one egg (listed with a question mark) near Sable Island.

[5] According to Sparks, three tows were taken at each station: No. 5 net, about 7 meters deep; No. 0 net, 0–2 meters deep; No. 0 net, 23–27 meters deep.

place occasionally on the western coast of Newfoundland, but probably only in bays in which the water warms up to 10° C. (50° F.); perhaps it is of irregular occurrence and it is certainly of minor importance.

Season.—In the southern half of the Gulf of St. Lawrence, eggs were present as early as May 29 and as late as August 12. The maximum catches were taken on June 30, July 7, and July 8, and it may be presumed that the height of the season was in the latter part of June and early part of July.

Relative Importance of the Several Spawning Regions

Because it is important to know which grounds are mainly responsible for recruitment of the mackerel population, an appraisal of the relative amounts of spawning in the four regions will be attempted, even though the available information is not adequate for precise treatment. Since these four regions are roughly equal in size and each is sufficiently large to constitute a major spawning area, it will suffice to examine only average concentration of eggs in each region. The pertinent data, in terms of average or usual number of eggs taken per positive surface tow with a meter net are as follows:

Continental shelf between Cape Cod and Cape Hatteras	3,000 to 5,000
Gulf of St. Lawrence	About 300.
Gulf of Maine (exclusive of Cape Cod Bay)	Less than 100.
Coast of Nova Scotia	About 14.

Of course, these numbers cannot be taken at their face values for there are many factors affecting their comparability. However, the last two items in the list are so low that it may be concluded that the coast of Nova Scotia and the Gulf of Maine are of negligible importance as mackerel spawning areas.

On the other hand, the Gulf of St. Lawrence and the continental shelf between Cape Cod and Cape Hatteras are both grounds of evidently some importance, and their comparison with each other deserves more careful consideration. The two things that might affect most obviously the comparability of the data on them are: (1) the technique of towing, including the distribution of stations, (2) the fact that the Gulf of St. Lawrence survey took place more than a decade earlier than the townetting over the continental shelf between Cape Cod and Cape Hatteras.

The techniques employed in the Gulf of St. Lawrence by the Canadian Fisheries Expedition obviously were not intended for quantitative purposes. According to Dannevig (1919, p. 3) "The duration of the surface hauls varied somewhat, as a rule between ten and fifteen minutes; * * *" and Huntsman (1919, p. 407) states, "The tow hauls (as distinguished from the vertical hauls) are the most unreliable, owing to lack of information in the records as to the manner in which they were taken * * *. The tow hauls were taken in a great variety of ways." Further, Huntsman's table (loc. cit., p. 419) of hauls by the C. G. S. *No. 33*, which contributed most of the mackerel eggs, shows that some of these hauls in reality were oblique and that towing periods varied between 5 and 20 minutes, with the time not given for certain of the hauls containing important numbers of mackerel eggs.

Furthermore, the stations were closely spaced in some portions of the Gulf and widely spaced in others. They may have chanced to be concentrated where the eggs were thickest or the contrary. Similarly, the distribution with respect to time may have been favorable to the taking of abnormally large numbers of eggs, or the contrary. On the other hand, the coverage, both as to space and time, was far from haphazard. The *Princess* occupied stations in the Gulf of St. Lawrence during June 9 to June 15 and again during August 3 to 12, and, in the meantime, *No. 33* was making net hauls in the southern half of the Gulf during June, July, and August, the two boats together making about 50 net hauls in the productive southern half of the Gulf during the mackerel spawning season (Dannevig, 1919, charts and tables).

While it cannot be said whether more intensive work over a more uniform pattern of stations would have revealed substantially a greater or less number of eggs than was taken by the Canadian Fisheries Expedition, the fact remains that only one of their hauls yielded more than a thousand eggs and only a few, more than a hundred. Experience in the area between Cape Cod and Cape Hatteras indicates that a similar coverage, with similar techniques, would have resulted in many more hauls containing thousands of eggs, and the conclusion appears inescapable that eggs were much less abundant in the Gulf of St. Lawrence in 1915 than in the area between Cape Cod and Cape Hatteras during 1927 to 1932.

It is difficult to determine how much the decade of difference in the time that the Gulf of St. Lawrence and the area between Cape Cod and Cape Hatteras were investigated affects the comparability of the data on egg numbers, but at least two obvious features may be considered—annual fluctuations and long-term trends in volume of spawning. In the area between Cape Cod and Cape Hatteras the numbers of eggs were consistently high during the years 1927 and 1932. Though the methods of towing varied too much and the coverage in some years was too deficient to permit mathematical demonstration of this, in every year the eggs were sufficiently abundant to be taken by the several thousand per surface tow at favorable times and in favorable places; and it may be concluded that annual fluctuations were not sufficient to alter the general magnitude of egg production. It appears also that the numbers of spawners, judging from catch statistics, did not fluctuate by orders of magnitude during this period. Thus, experience suggests that the egg yield does not fluctuate markedly as long as the number of spawners does not.

Referring now to the catch statistics in the Canadian and the United States fisheries (Sette and Needler, 1934, p. 43) it appears that the trend in Canada was nearly horizontal between 1915 and the late 1920's, but that in the United States the general level was about three times as high in 1929 as in 1915. If it may be assumed that the spawners are, in general, proportional to the catch and that the numbers of eggs are proportional to the number of spawners, both of which are admittedly questionable premises, then it could be argued that the 1915 Canadian data on eggs would roughly hold for recent times and the comparison justified as indicating relative amounts of spawning in the two areas in recent times. On the other hand, comparison as of 1915 might be expected to reduce by two-thirds the numbers of eggs in the Cape Cod to Cape Hatteras area, and thus indicate relatively greater importance for the Gulf of St. Lawrence. Even so, the change would not be one of order of magnitude.

All available information considered, it appears most likely that the spawning in the area between Cape Cod and Cape Hatteras is distinctly more important than in the Gulf of St. Lawrence, and though it is possible that the difference is one of an order of magnitude, with eggs so concentrated in the Cape Cod to Cape Hatteras region as to be available in the thousands per tow, and so scarce in the Gulf of St. Lawrence as to be available in the hundreds per tow, it is also possible that the true divergence is less marked and that the numbers are really in the upper and lower levels of the same order of magnitude. The diagrammatic representation of relative egg numbers in the various regions given in figure 3 should be considered with this reservation. Although the collection of more adequate data on the subject is greatly to be desired, present information supports the view that the present survey has covered the most important spawning ground.

The existence of large regions with little spawning near the middle of the spawning range of the species is a peculiarity that may be explained by hydrographic conditions. It will be noted from the diagrammatic representation of relative intensity of spawning in figure 3 that the regions of greatest intensity are the southern and northern quarters of the spawning range. That of the least intensity is the middle half of the range. The places of intense spawning, that is, the great oceanic bight between Cape Cod

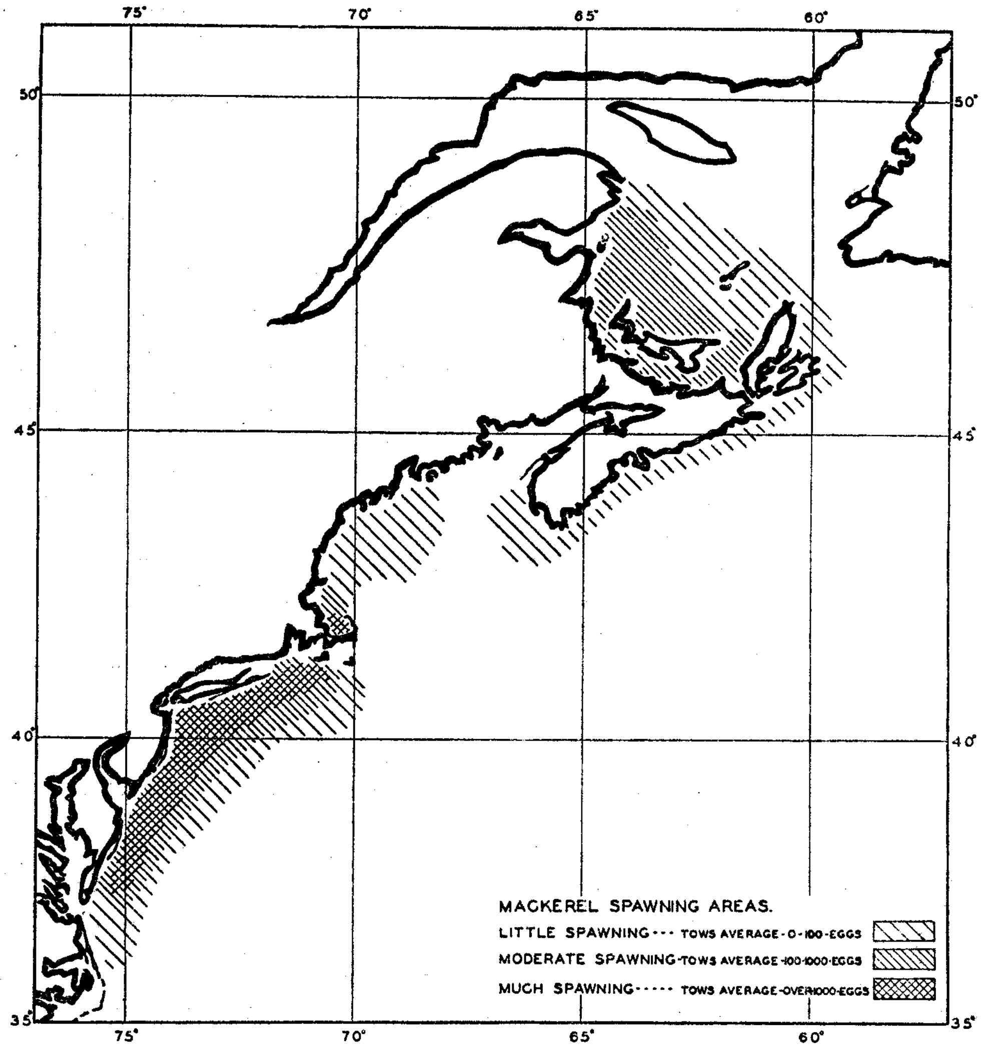

FIGURE 3.—Relative intensity of mackerel spawning in various regions along the Atlantic coast of North America, as indicated by the average number of eggs caught in plankton nets.

and Cape Hatteras, Cape Cod Bay, and the southern half of the Gulf of St. Lawrence, have this in common: they are all bodies of relatively shoal water overlying relatively flat bottom, where topography and circulation favor vertical stability, and vernal warming of the upper strata proceeds rapidly, producing temperatures suitable for mackerel spawning earlier than in the intervening areas. On the other hand, the places of least intense spawning are areas with broken bottom where tidal and general circulation produce extensive vertical turbulence, drawing cold water from the depths to the surface, thereby delaying the vernal warming of the upper strata, as a rule, until the mackerel spawning season is over. As nearly as may be determined from the information on hydrographic conditions (Bjerkan, 1919, pp. 379–403, Bigelow, 1928, pp. 550–585) and on spawning times and places (see above), the dividing line between good and poor spawning areas may be drawn at a vernal temperature of about 8° C., (46° F.). The areas that receive little or no spawn are, during the spawning season, usually colder, and those that receive much spawn are usually warmer than this temperature.

NUMBER OF EGGS SPAWNED AND SIZE OF SPAWNING STOCK

A rough estimate of the total number of eggs spawned in the region between Cape Cod and Cape Hatteras can be made from the data of the 1932 survey of spawning. The average catch during the first seven cruises was about 1,000 eggs per 17 square meters of sea surface (table 19), or an equivalent of about 200 million eggs per square nautical mile. Taking 25,000 square miles as the areas surveyed, this would amount to a total of 5,000 billion eggs. Since this figure is based on the average concentration during a 50-day period, and since the period of incubation would average about 7 days at the prevailing temperature, there must have been about 7 renewals or approximately 35,000 billion eggs spawned to maintain this average concentration. From a curve of numbers of eggs taken in successive cruises, it appears that perhaps one-seventh should be added to allow for the fact that the cruises did not begin early enough or extend late enough to include all the spawning. This raises the figure to 40,000 billions eggs. These are in all stages, and it may be computed from mortality rates of eggs (table 7) that this would be equivalent to 1.6 times as many newly-spawned eggs. Applying this factor, the final estimate of eggs spawned in this area in 1932 becomes about 64,000 billion.

It is difficult to appraise the reliability of this estimate because of the uncertainty of its components. Judging these as well as may be, it appears that at best it may be within 25 percent of the true value and at worst only within the true order of magnitude. But this is only personal judgment, and since it is impossible to study statistical probabilities, there is utility in testing the result by deriving a related statistic from an entirely different source.

During 1932 the catch of mackerel on or near spawning grounds during the spawning season; that is, in area XXIII (Fiedler, Manning, and Johnson 1934, p. 96), and in area XXII, west of Nantucket Shoals during April, May, and June, was about 13,000,000 pounds. From unpublished records on size composition of this catch, it appears that about 10,000,000 pounds of it consisted of fish of spawning size, and that their average weight was nearly 1.9 pounds. Thus, a take of about 5,000,000 spawners is indicated.

To estimate from this the size of the spawning stock it is necessary to know what percentage this was of the spawning stock in 1932. This may be done only in an indirect manner. The 1923 class of mackerel, after reaching spawning age, declined at a rate of 20 percent per year as measured by the catch per purse seine boat during the four seasons, 1928 to 1931 (Sette, 1933, p. 17). This decline was so steady that it probably should be ascribed to mortality rather than to other causes, such as changes in availability. Of course one cannot be sure that the spawning population in 1932 was subject to the same mortality as the 1923 class during the previous years, but as far as the intensity of fishing is concerned, there was no significant change between 1931 and 1932. The fleet numbered 112 seiners in 1931 (Fiedler, 1932, p. 211) and 114 in 1932 (Fiedler, Manning, and Johnson 1934, p. 97).

Views may differ as to the relative part played by catch mortality and by natural mortality in causing total mortality, but by taking divergent views, say three-quarters catch mortality on the one hand and one-quarter catch mortality on the other hand, one would arrive at 15 and 5 percent, respectively, as catch mortality; or, taking a middle ground, it would be 10 percent. Similarly divergent views may be taken as to the fraction of annual mortality suffered during the spawning season. Perhaps three-quarters and one-quarter, respectively, may reasonably be taken as the extremes and one-half (or 10 percent) as the middle ground. These would give as extremes 11 and 1.25 percent that the catch during the spawning season was of the total spawning stock. The middle view would be 5 percent.

This results in an estimated total population between 45,000,000 and 400,000,000, with a middle ground estimate at 100,000,000 individuals in the spawning population on the spawning grounds as derived from catch statistics.

It will now be recalled that the estimate derived from tow net hauls was 64,000 billion eggs spawned, and if 400,000 eggs are produced by the average female (p. 156) the indicated spawning population would be 160,000,000 females, or 320,000,000 fish of both sexes. This is within the extremes computed from the catch data and about halfway between the middle and largest figures. Considering the approximate nature of some of the elements in the estimates, this is a remarkable agreement between the two methods of computing the size of the spawning stock, and strengthens the view that the total estimate of eggs is sufficiently reliable to warrant the conclusion that the egg production was in the order of 50,000 billion in 1932.

This, of course, refers only to the spawning in the region south of Cape Cod, and it has been pointed out (p. 160) that important spawning occurs also in the Gulf of St. Lawrence. Since spawning in the latter region seemed to be of lesser magnitude than south of Cape Cod, it is probable that the entire spawning off the east coast of North America would not be more than double the estimated 64,000 billion, or, since the latter is an uncertain figure, let us say in the order of one hundred thousand billion eggs.

SPAWNING HABITS

According to Bigelow and Welsh (1925, p. 208), "Mackerel spawn chiefly at night." If this be true, the earliest egg stages should be relatively more abundant at certain times of the day than at others. From material collected at a number of stations in 1929, the eggs in "early cleavage" and "late cleavage" were counted, representing respectively the first and second 10 hours of development at the temperatures prevailing at the time. If spawning took place chiefly at night the early cleavage eggs should predominate between midnight and 10 a. m. and be in the minority during the remainder of the day. At the 14 stations from each of which more than 10 eggs of both stages were examined, the average percentage of early cleavage in the midnight to 10 a. m. group was 45 and in the 10 a. m. to midnight group 33. The difference between the two groups was not statistically significant (t=0.91 and P=0.3 +, according to the method of Fisher, 1932, p. 114) and it may be concluded that the diurnal variation in percentage of early stage eggs does not indicate a tendency toward more spawning by night than by day. Tabulation of percentages according to the hours of the day did not indicate that any other particular part of the day was favored.

THE EGG

Description.—According to published descriptions, (Ehrenbaum, 1921, p. 4 for the European mackerel; Dannevig, 1919, p. 11, and Bigelow and Welsh, 1925, p. 208, for the American mackerel) the mackerel egg is 0.97 to 1.38 mm. in diameter and contains an oil globule 0.28 to 0.35 mm. in diameter. Measurements of eggs taken at sea during this investigation had a similar range in dimensions. By far the commonest dimension (modal) was 1.2 to 1.3 mm. for the egg and 0.31 to 0.32 mm. for the oil globule.

There is a tendency toward a decrease in size of mackerel eggs as the season advances. Data given by Ehrenbaum (1921, p. 4) show the same tendency in the egg of the European mackerel. This could be due to the seasonal trends of either temperature or salinity, but the experiments of Fish (1928, pp. 291–292), who found cod eggs fertilized in cold water to be larger than those fertilized in warm water, suggest that temperature alone could be responsible. Whatever its mechanism, the phenomenon of decrease in size as the season advances probably holds true for all species occuring in the tows of the present investigation. It was my practice to make scatter diagrams in which oil globule diameter was plotted against egg diameters for all eggs in hauls containing troublesome mixtures. Invariably, when mackerel eggs were near the limits of the over-all range of their dimensions and thus might be expected to overlap the range of the eggs of other species, the latter were also near the corresponding limits of their respective over-all range and the groups remained discrete, showing that tendencies for smaller or larger than average size were shared simultaneously by all species. Thus, in individual collections the range in dimensions was much less than the relatively large range of all collections, and a feature that might have been a hindrance in identification was in reality not very troublesome.

In the collections made during the course of this investigation there were eggs of four species whose dimensions approached those of the mackerel. The egg of the common bonito (*Sarda sarda*) is 1.15 to 1.33 mm. in diameter, but in its early stages it has a cluster of small oil droplets instead of a single large one. In its late stages, these droplets often become united into a single oil globule. In this condition there might be some difficulty in distinguishing the two, were it not that bonito eggs occur later in the season (in areas we have prospected) when the mackerel eggs are considerably smaller. For instance: Mackerel eggs taken in Cape Cod Bay, July 19, 1929, were 1.00 to 1.12 mm. in diameter while bonito eggs taken July 25, 1929, in the offing of No Man's Land were 1.12 to 1.27 mm. in diameter. The eggs of the cusk (*Brosmius brosme*) and the tilefish (*Lopholatilus chamaeleonticeps*) are similar in size but have oil globules distinctly smaller (0.19 to 0.23 mm.) than those in the mackerel's eggs. Closer to the mackerel egg in its dimensions was that of a species not yet identified. Although overlapping the mackerel egg in dimensions, its modal size was distinctly smaller and the oil globule somewhat larger, and in its late stages the embryonic pigment was arranged in bars unlike the diffuse arrangement in the embryo of the mackerel. Inasmuch as eggs of this type were found only at the edge of the continental shelf, their distribution was discontinuous with that of the mackerel; and since no mackerel larvae were later found in the same or neighboring localities this egg caused no confusion.

Rate of embryonic development.—Although mackerel have never been observed in the act of spawning, it is generally supposed that both eggs and sperm are discharged into the surrounding water, where fertilization takes place. Observations have shown that thereafter, during the period of embryonic development,[6] the eggs are suspended in the sea water mostly near the surface and all above the thermocline.

As is true with most cold-blooded organisms the rate of development depends on the temperature at which it takes place, being slower at low temperatures and faster at high temperatures. According to Worley (1933), who examined this feature of the development at the U. S. Fisheries Biological Station, Woods Hole, Mass., the time elapsing between fertilization and hatching was 50 hours at 21°, 70 hours at 18°, 95 hours at 16°, 115 hours at 14°, 150 hours at 12°, and 208 hours at 10°. There is no reason for believing that the rates differ at sea, though this is difficult to demonstrate.

According to Worley (1933, p. 857), "Experiment showed that typical development (and survival) could be realized only between 11° and 21°." At sea in 1932, however, eggs were most abundant at temperatures below 11°, as appears from the following average numbers taken at each degree (centigrade) of surface temperature encountered in the survey:

7	0	14	150
8	111	15	555
9	2, 117	16	44
10	3, 360	17	5
11	2, 432	18	74
12	1, 390	19	0
13	1, 380	20	0

The embryos in eggs from water below 11° C. differed in no perceptible way from those found in warmer water, and there is no reason for believing that development was not proceeding as "normally" at the lower as at the high temperatures.

Worley also found (loc. cit.) that "The total mortality during the incubation period was least at 16° C. where it amounted to 43 percent." He had three experiments at this temperature with mortalities of 37, 40, and 53 percent respectively (loc. cit. p. 847). At sea, in 1932, the average mortality was 59 percent (from interpolation to the hatching point from the data of the 5th column in table 7), or only a little greater than in the least favorable of the laboratory experiments. The weighted mean temperature of the water from which these sea-caught eggs were taken was 10.9° C. Worley's laboratory eggs suffered 90 and 95 percent mortality in his two experiments at 11°.

Obviously, both the range for normal development and the point of maximum survival were at lower temperatures at sea than in the laboratory experiments of Worley. The explanation for this disparity between results in the laboratory and observations at sea probably lies in the fact that Worley's experiments took place at a time when temperatures of the sea water from which he took his fish were in the neighborhood of 16° C. The lesser mortality at and near this temperature was connected no doubt with the lesser change involved in bringing the eggs from the temperature of the parent to the temperature of the experiment. It is obviously desirable that laboratory experiments be repeated on material taken from water of lower temperature.

Vertical distribution.—Although it has been known that mackerel eggs are suspended in the sea, usually near the surface, there has been in American waters no previous determination of vertical distribution, apart from the general observation

[6] For the minutiae of the embryology of mackerel, the reader is referred to Moore (1899, pp. 5-14), and to Wilson's (1891) description of the sea bass, which the mackerel in its embryology closely resembles.

that surface hauls take more eggs than deeper hauls. The present determination is based on a series of horizontal hauls at different depths in 38 meters of water in the offing of the Fire Island Lightship on May 19, 1929.

Four series were taken: one at dawn, another at noon, another in the evening, and the final series at midnight. The net was one-half meter in diameter at the mouth and rigged with a closing device actuated by a messenger. It was lowered while open, towed for 20 minutes, then closed and hauled to the surface. Each series included hauls at the surface and at the 5-, 10-, 20-, and 35-meter depths. The courses of the nets were kept as nearly horizontal as possible by periodical estimation of depth based on measuring the towing warp's angle of stray and paying out or hauling in the line as needed to keep the net at the proper level. Since the net was lowered while open, and since the tripping mechanism failed on several occasions, there was some contamination of the haul during its passage through the water overlying the stratum fished. Correction for this contamination was estimated on the basis of the average concentration of eggs in the overlying water and the time it took the net to pass through the overlying water in an opened condition. An additional correction for variations in speed of towing, based on the angle of stray of the towing warp, was applied to all catches on which data adequate for this purpose were available.

TABLE 2.—*Vertical distribution of mackerel eggs at station 20498, May 17, 1929*

Depth	Numbers taken per haul				Numbers per haul adjusted to standard [1]			
	Dawn	Noon	Sunset	Midnight	Dawn	Noon	Sunset	Midnight
Surface	12,080	34,600	27,900	13,320	[2] 12,080	[2] 32,900	[2] 27,900	[2] 13,320
5 meters	10,810	13,210	21,600	13,200	13,880	17,900	[2] 22,850	[2] 13,145
10 meters	11,120	8,850	8,750	8,260	7,550	8,210	11,480	[2] 7,600
20 meters	5,120	1,070	380	694	[3] 2,960	750	0	[2] 418
35 meters	1,182	20	124	285	0	0	0	[2] 15

[1] Adjusted for time (20 minutes); speed (to cause stray of 28.5° in towing wire); and for contamination in passing through overlying strata in paying out and hauling in.
[2] Not adjusted for speed.
[3] Adjustment for contamination was large and probably inaccurate.

As may be seen from figure 4, the numbers decrease rapidly with depth. When the numbers from the several hauls at each level (exclusive of certain unreliable subsurface hauls designated as questionable in the figure) are averaged, the distribution is as follows: surface, 22,000 per haul; 5 meters, 13,000; 10 meters, 8,000; 20 meters, 700; 35 meters, 0. Except for the surface hauls which were not adjusted for towing speed, and certain of the subsurface hauls on which reliable corrections were impossible, the successive hauls at each level yielded nearly the same numbers, indicating at once the reliability of the method of sampling and the stability of the vertical distribution.

Comparing the distribution of eggs with physical conditions, it is obvious that eggs were abundant from the surface down to a depth of 10 meters, the range in which temperature, salinity, and therefore density were approximately uniform. Between 10 and 20 meters the temperature decreased sharply, the salinity increased sharply, and therefore the density increased sharply. In this zone of increasing density, the mackerel eggs rapidly diminished in number so that at 20 meters few were taken and below 20 meters, none. At this station, therefore, the distribution of mackerel eggs was limited to the stratum above the pycnocline (zone of sharp increase in density).

While this has been demonstrated in detail at only this one station, that it is a general rule is indicated by subsequent experience with oblique hauls, where, with several nets on the line, the deeper nets, when towed entirely below the thermocline, took very few eggs that were not otherwise accounted for (by the contamination correction based on the average catch of the upper net and on the time taken to pass through the upper stratum). It is safe to conclude therefore, that the pycnocline forms a barrier to the downward extension of mackerel eggs. Further, the pycnocline is sufficiently well indicated by the thermocline in this region so that the latter may be used an an indicator of the lower limit of mackerel eggs.

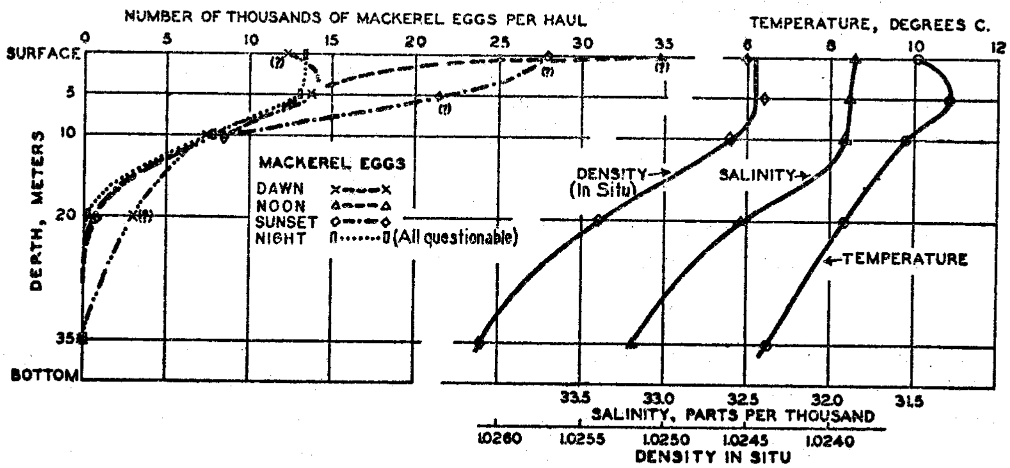

FIGURE 4.—Vertical distribution of mackerel eggs in relation to temperatures, salinity, and density of water. Observations were adjusted to the basis of standard speed of towing, except those indicated as questionable.

The serial tows of May 17, 1929, also illustrated significant differences in the vertical distribution of eggs in different stages of embryonic development. When the eggs were separated into three stages of development occupying approximately equal periods of time, it was found that those of the early stage (A) were mostly near the surface, those of the late stage (C) mostly between the 5- and 10-meter levels, and those of the intermediate stage (B) intermediate between A and C in their vertical distribution (table 3). Too few eggs were taken at greater depths to indicate reliably the proportionate numbers at each of the three different stages of development.

TABLE 3.—*Vertical distribution of various stages of mackerel eggs according to noon series, station 20498, May 17, 1929*

[Stage A is from fertilization to complete epiboly; stage B is from complete epiboly to embryo extending three quarters around the circumference of the egg; stage C is from this point to hatching]

Depth	Number taken				Number adjusted to standard [1]			
	Stage A	Stage B	Stage C	Total	Stage A	Stage B	Stage C	Total
Surface	30, 250	4, 250	100	34, 600	29, 630	4, 170	100	33, 900
5 meters	3, 960	5, 690	3, 560	13, 210	5, 280	7, 760	4, 860	17, 900
10 meters	980	2, 950	4, 920	8, 850	800	2, 750	4, 660	8, 210

[1] Adjustments the same as in table 2.

The differential vertical distribution of the several egg stages could result either from a decrease in specific gravity of the water after the eggs were spawned or an increase in the specific gravity of the eggs as embryonic development proceeded. Moore (1899, p. 14) concluded that the eggs increased in specific gravity during development when he noted that mackerel eggs which he was incubating in the laboratory sank during the third day. But he gives neither the specific gravity of his 3-day-old eggs [7] nor that of the sea water either at the beginning or end of his experiment. Since he was working before rigid control of temperature was customary, it is likely that the specific gravity of the water in his experiment may have been changed by warming.

In the present example, at least, it is known that the temperature of the water was increasing at the time station 20498 was visited. At the temperature of the water in which the eggs were found on May 17, it takes about 5 days for incubation (p. 167), and it may be estimated that stage C eggs were spawned at least 3 days prior to stage A eggs, hence on May 14, when unfortunately this station was not visited. However, from interpolation (linear) both in space and time between the temperature at station 20498 on May 17 and temperature at neighboring stations on May 12, it appears that the density of the water at the surface on May 14 could have been very nearly the density of the water at the 10-meter level on May 17. Hence it is preferable to ascribe the sinking of the late stages to the warming of the water with attendant decrease in density, rather than to an increase in the density of the eggs.

THE LARVA [8]

Yolk-sac stage.—The newly hatched larva [9] is slightly less than 3 mm. in length, well covered with scattered black pigment spots which tend to be denser dorsally than ventrally. The eyes are colorless. The region of the gut is occupied by the yolk sac with its oil globule. Both sac and globule are about the same size as they were in the egg. The mackerel is readily distinguished from other similarly marked larvae with which it is found, by its larger size, stouter shape, coarser pigment spots, and its 30 myomeres.

As development proceeds, the pigment becomes localized on top of the head and along dorsal and ventral edges of the body, the eye becomes black, the yolk sac absorbed, the mouth and gut formed. These changes are completed at a length of 4 mm.

As seen in the laboratory and hatchery, the mackerel swim very feebly during the yolk-sac stage, with short, spasmodic, random movements. Their balancing faculty is undeveloped, their position being indifferently upside down, right side up, and at various angles. At sea they must be totally at the mercy of the water movements.

Larval stage.—As used herein, this stage represents the period beginning after yolk-sac absorption and ending after fin formation, and it includes individuals between 4 and 8 mm. in length. In this stage, the mackerel is readily distinguished from other species by the row of black spots of irregular size and spacing along dorsal and ventral edges of the body, beginning about midway between snout and tail and extending almost to the end of the notochord (but not into the fin fold). Those in the dorsal row are less numerous and more widely spaced than those in the ventral. Other species which were found with the mackerel, and which have also such dorsal and ventral rows of pigment, are the winter flounder (*Pseudopleuronectes americanus*), which differs from the mackerel by its greater number of myomeres (37–40) and its

[7] But he does give the specific gravity of newly spawned eggs as between 1.024 and 1.025, a figure very close to that of surface water at our station 20498. (See fig. 4.)

[8] While the term larva may be applied to the entire planktonic existence, it is convenient to recognize three subdivisions: yolk-sac stage, larval stage, and post-larval stage.

[9] This description is based on formaldehyde preserved specimens because this is the form commonly available for study. In life, the newly-hatched larva is longer, measuring 3.1 or 3.2 mm. (distortion and shrinkage decrease the length of preserved specimens), and in addition to the black pigmentation, have yellow and greenish pigment on each side of the head between the eye and otocyst, and on the surface of the oil globule (Ehrenbaum, 1905 p. 31).

strongly, laterally compressed body; the bluefish (*Pomatomus saltatrix*), which differs by its fewer myomeres (24); and the rosefish (*Sebastes marinus*), which has the same number of myomeres (30) and in the 4- to 5-mm. stage could be confused with mackerel. With both the rosefish and mackerel available for comparison, the former is readily distinguished by the closeness of the spots in the dorsal and ventral rows, those in the rosefish forming almost a continuous black streak, whereas those of the mackerel are discrete. Other differences, less useful, are the more slender shape and the greater relative length of the post-anal region in the rosefish larva. After passing the 5-mm. stage, the rosefish larva is readily separated from the mackerel larva by its prominent preopercular and cranial spines. An additional character of use in separating the mackerel larva from the others is its strong teeth, which are readily visible in specimens of the 7-mm. size but less so in smaller individuals.

Inability to keep larvae alive in the laboratory or hatchery during this stage precluded direct observation on their activity, but, as is shown in a later section, their movements are sufficiently well-directed for performance of diurnal vertical migrations of 20 to 30 meters but not sufficiently sustainable for migrations of miles in extent.

Transition phase.—Intervening between larval and post-larval stages is a transition phase including individuals 9 and 10 mm. long whose fins are in various states of completion.[10] Fin formation is a gradual process, neither beginning sharply at 9 mm. nor ending sharply at 10 mm. At the former length, the caudal fin already shows a number of rays, and at the latter length, the laggard first dorsal fin does not yet show any of its spines. But the tail fin makes its greatest changes, the second dorsal fin and finlets and the anal fin and finlets are all developed within this size range, hence it is most appropriately designated as a transition phase.

Post-larval stage.—This stage includes the latter part of planktonic existence beginning at about completion of fin formation and lasting until the young fish are nimble enough to evade the plankton nets. It is comprised of individuals 11 to 50 mm. long.

Since all the vertical fins except the first dorsal are complete, identification by adult characters is simple. The larvae enter this stage somewhat laterally compressed, and by its end fill out to the trim fusiform shape of the adult. At the beginning of this stage the color pattern is typically larval, but by its end the dark pigment has spread over the dorsal portions, and in live specimens the silvery hue is apparent, though the black wavy bands characteristic of the adult are yet to form. The appearance is in general like a miniature adult with somewhat oversized head and fins.

As appears in a later section, the post-larvae are capable of extensive swimming. Furthermore, as they near the end of this stage the schooling instinct asserts itself. The transition from a primarily planktonic habit to a primarily swimming and schooling habit probably is gradual, in the sense that all individuals may not experience the change at the same size. The available evidence is that it involves individuals between about 30 and 50 mm. in length. This evidence is from two sources. First, the survival curve (fig. 17) has a substantially uniform trend from 11 to 30 mm., from which it may be inferred that there was no change of trend within this size range sufficient to indicate a loss of larvae such as could be expected if some had begun to

[10] The present description of lengths at which fins appear differs from published figures (Ehrenbaum, 1921, figs. 1 to 7, and Bigelow and Welsh, 1925, fig. 92) probably because the latter give lengths inclusive of finfold or caudal fin, though this is not definitely stated; whereas our measurements were taken to the end of the notochord, i. e., exclusive of the finfold in early stages; and to the base of the caudal fin rays, i. e., exclusive of the caudal fin in later stages. This was necessary on account of frequent distortion or injury to the caudal appendage.

school and were no longer susceptible to capture in plankton nets. Second, a school of small mackerel was observed and sampled in Woods Hole Harbor in July 1926, containing individuals between 35 and 65 mm. in length (table 21). The first evidence shows that the schooling habit did not involve fish under 30 mm. in length; the second proves that some fish, at least, begin schooling as soon as they exceed that size.

Vertical distribution.—From series of horizontal hauls at 0, 5, 10, 20, and 35 meters at early morning, midday, evening, and midnight, at a station (*Albatross II* No. 20552) southeast of Fire Island Lightship (latitude 40°20′ N., longitude 70°57′ W.) visited on July 13 and 14, 1929, there is evidence that the larvae of the mackerel do not descend far below the surface, probably being limited by the thermocline, and that they perform a diurnal vertical migration (fig. 5).

TABLE 4.—*Vertical distribution of mackerel larvae at various times of the day as indicated by horizontal tows with a closing half-meter plankton net at Station 20552 (Albatross II), latitude 40°20′ N., longitude 72°59′ W., July 13 and 14, 1929*

Depth of haul	Time [1]	Length of larvae (millimeters)						Total	
		4	5	6	7	8	9		
		Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Percent*
Dawn:									
Surface	2.53 a. m.			2	2		2	6	93
5 meters	3.27 a. m.	1						1	7
10 meters	3.54 a. m.							None	
20 meters	4.20 a. m.							None	
35 meters	6.03 a. m.							None	
Total		1		2	2		2	7	100
Noon:									
Surface	11.33 a. m.							None	
5 meters	12.08 p. m.							None	
10 meters	12.24 p. m.							None	
20 meters	12.52 p. m.							None	
35 meters	1.17 p. m.							None	
Evening:									
Surface	6.26 p. m.		2					2	14
5 meters	6.51 p. m.							None	
10 meters	7.17 p. m.	1	10	13	1			25	86
20 meters	7.44 p. m.							None	
35 meters	8.12 p. m.							None	
Total		1	12	13	1			27	100
Midnight:									
Surface	11.30 p. m.		1	4	5	1	1	12	38
5 meters	11.54 p. m.	1	13	2	1			17	53
10 meters	12.22 a. m.		2		1			3	9
20 meters	12.47 a. m.							None	
35 meters	1.13 a. m.							None	
Total		1	16	6	7	1	1	32	100

[1] Midpoint of the 20-minute haul is given.

In detail it will be noted (table 4) that in any one series of hauls the larvae were caught mostly at only one or two levels; indicating that they were confined to such thin strata that the entire population could easily, at times, be situated between the levels of the hauls, and hence at those times be missed. Accordingly, it is probable that in the evening the larvae were nearly all at the 10-meter level, probably traveling upward, and by midnight some had reached the 5-meter level and some the surface. The deeper ones probably continued upward so that nearly all reached the surface shortly after midnight; and by 3 a. m., when the next series began, they had begun to descend so that they were between the surface and the 5-meter level, and few were taken in the hauls at either level. By noon, they probably had descended beyond 10 meters and were located between the 10 and 20 meter hauls, and none was caught.

It is improbable that the daytime descent was beyond the 20 meter level at this station or was ever beyond the thermocline. During 1930, 1931, and 1932, when the nets were hauled obliquely below as well as above the thermocline, the lower tows seldom caught larvae that could not be accounted for as contaminants resulting from passage through the upper layers.

From the length-distribution of the larvae it appears (table 4) that the larger individuals (6 to 9 mm.) were more stongly inclined to migrate, reaching the surface at night, while the smaller ones (4 to 5 mm.) tended to stay in the intermediate 5- to 10-meter levels.

Though these observations do not provide a precise description of vertical distribution and migration, they do demonstrate the necessity of sampling all levels down to the thermocline to get the representative statistics needed for the studies on growth and mortality to follow.

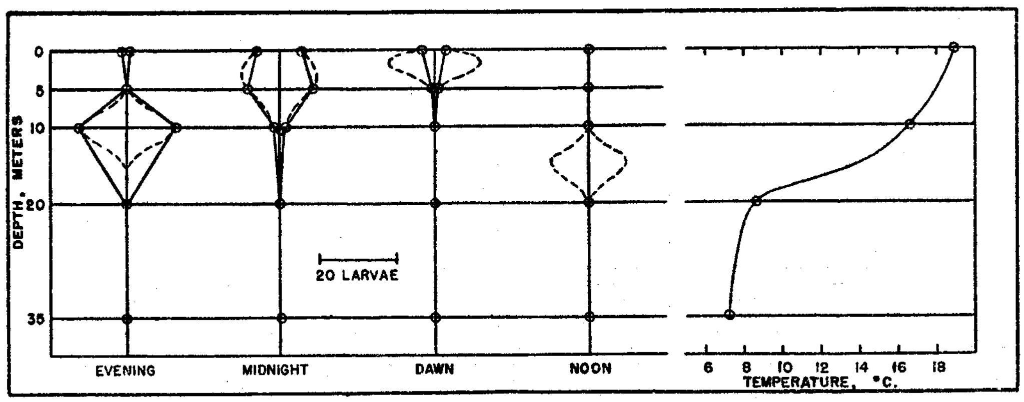

FIGURE 5.—Vertical distribution of mackerel larvae at several points of time in the dirunal cycle in relation to temperature. The solid lines connect observational points. The broken lines indicate the probable vertical position of the bulk of the population of larvae.

GROWTH

Very little has been published on the growth of marine fishes during that early period of the life history spent in the plankton community, and nothing on the growth of the mackerel during this stage. Of the data collected during the present investigation, only those of 1932 were collected in a manner sufficiently quantitative and at short enough intervals of time to be used in deducing growth rate.

The method of analysis consists, essentially, in following the advance in position of the mode of homologous groups of larvae by comparing sizes collected in successive cruises. But this cannot be done in a simple and direct manner. Mackerel eggs are spawned over a period of several months. The larvae are subject to high mortality. As a result, almost always there are vastly more small larvae than large ones, and the predominance of small larvae is so great during most of the season that the groups of larger ones do not form distinct modes. Instead, in ordinary arithmetic frequency distributions they are apparent principally as a lengthening of the "tail" of the distribution at its right-hand side (table 5).

TABLE 5.—*Number of eggs and larvae taken on each cruise in 1932, classified according to stages of eggs and lengths of larvae*

[During cruises 1 to 7, tow nets 1 meter in diameter at mouth were used, and during cruises 8 and 9, tow nets 2 meters in diameter were used; all hauls were obliquely towed and numbers caught were adjusted to represent an equal amount of towing per meter of depth fished]

Egg stages and lengths of larvae in millimeters	Cruises								
	I May 2-6	II May 9-16	III May 19-23	IV May 24-28	V June 1-5	VI June 5-8	VII June 15-21	VIII June 25-July 1	IX July 16-24
A	11,415	21,563	22,294	12,172	2,907	2,815	851	(1)	(1)
B	7,895	13,585	13,519	15,287	2,057	1,161	1,303	(1)	(1)
C	4,667	18,228	5,266	21,712	6,011	1,562	2,733	(1)	(1)
3	4,017	6,310	7,338	18,392	5,215	9,214	8,805	[1] 0.3	[1] 1.6
4	1,690	838	2,207	[2] 4,462	1,243	8,236	734	[1] 0.4	[1] 12.5
5	239	751	1,607	[2] 751	1,049	2,371	546	[1] 5.6	[1] 8.9
6	38	311	544	[2] 200	1,132	501	208	[1] 15.9	[1] 11.4
7	12	21	151	[2] 25	911	399	55	36.6	8.9
8	4	2	40	[2] 48	200	470	19	30.1	17.2
9	1	1	18	[2] 28	54	186	13	16.6	8.2
10			7	[2] 3	7	41	12	9.6	3.4
11			5	[2] 2	6	12	5	5.8	1.9
12					2	4	9	3.8	1.2
13					1	4	7	.8	.1
14					2	2	8	1.1	.4
15						1	5	.6	.3
16							2	.5	.8
17							3	.2	.1
18							5	.1	
19							3	.2	.1
20							1	.3	.3
21							1		.5
22							1	.1	.3
23									1.3
24									.3
25									.8
26									1.0
27									1.3
28									1.3
29									
30									.3
37									.3
51									.1
Total	29,978	61,610	53,006	73,082	20,797	26,979	15,329	128.6	84.8

[1] Eggs and larvae below 7 mm. were not retained in their full numbers by the coarse-meshed nets used on cruises 8 and 9.
[2] The numbers given in this class are deficient, due to failure to occupy the usual number of stations at the southern end of the area of survey where many of the larvare of this size were to be found at this time. For revised data see footnote on p. 192.

The groups of more than average abundance were brought into prominence by a modification of the conventional deviation-from-average-frequency method. The average numbers per cruise of the larvae at each length ("observed values" of table 6) were converted to logarithms and plotted against logarithms of lengths. Straight lines were fitted to these observed values (figure 6) from which the theoretical values were derived. These were subtracted from the logarithms of the frequencies of each cruise, giving remainders which represent the relative amounts by which the number of larvae of particular sizes deviated from the average number at particular times in the season (last 9 columns of table 6).

Since the average curve was, in effect, an estimate of mortality by sizes, the deviations may also be regarded as frequencies from which the effect of mortality was removed, leaving only the effects of rate of hatching, rate of growth, and, of course, the random variations of sampling. Fluctuations of hatching (resulting from fluctuations in spawning) give rise to modes, and growth causes the modes to progress from one cruise to the next. If early growth of the mackerel is exponential as in many animals and plants, the progress of modes should be along straight lines when the deviations are plotted against logarithms of length, as in figure 7. This idea influenced the selection of homologous modes marked by corresponding letters R, S, and T, in the figures.

That each series includes truly homologous groups is indicated by several criteria, independent of the straight-line conformity. In the R series, the modes all tend toward peakedness. In the S series, they all tend to be broad. In the T series they are intermediate in shape. The progress in each series is reasonably consistent and the course of growth is roughly parallel in the three series; moreover, the slight departure from parallelism is in the expected direction, the later series having the higher growth rates consistent with their development in the warmer water to which they are subjected. Furthermore, the modes are consistently present in the material from each cruise with only two exceptions, R in cruise III and S in cruise IV. The absence of S in cruise IV is plainly due to failure on that cruise to visit certain stations in the southerly end of the spawning area, where previous cruises would lead one to expect

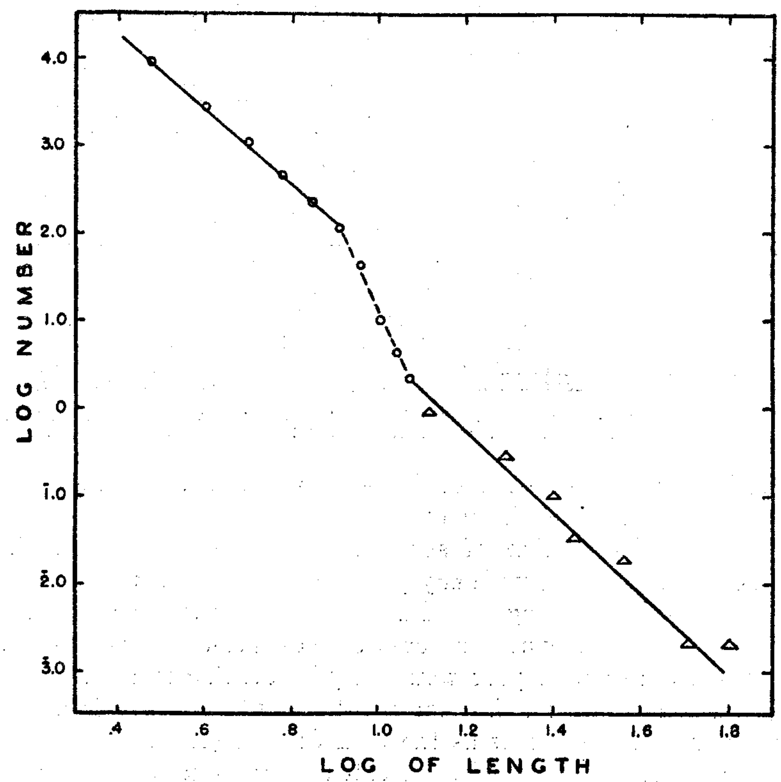

FIGURE 6.—Frequency distribution of lengths of larvae plotted logarithmically.

to find larvae of sizes appropriate for this series (fig. 13, IV). Absence of R in cruise III has no such simple explanation, and can be explained only as chance sampling fluctuation.

Only one other reasonably sensible alternative to the series of homologies in figure 7 is possible. According to this alternative, R of cruises I and II would be considered forerunners of the 9- and 10-mm. larvae of cruise III; S of cruise III considered the forerunner of R of cruises V and VI; the 3- and 4-mm. larvae of cruise IV, the forerunner of S of cruise V; S of cruises V and VI, the forerunner of R of cruise VII; and T of cruise VI, the forerunner of S of cruise VIII. But, this would not account for the presence of such prominent modes as R of cruise IV, S of cruise VII, or T of cruise VIII; and there are other objections to this alternative set of homologies which will be considered later.

TABLE 6.—*Deviations of individual cruise frequencies of lengths of larvae and postlarvae from the average frequency* [1] *of the 9 cruises of the season of 1932*

Length		Average number per cruise			Cruises								
		Observed values [2]		Theoretical values [1]	I	II	III	IV	V	VI	VII	VIII	IX
Mm.	*Log*	*Number*	*Log number* [3]	*Log number* [3]	*Dev.*	*Dev.*	*Dev.*	*Dev.*	*Dev.*	*Dev.*	*Dev.*	*Dev.*	*Dev.*
3	0.477	8,470	13.93	14.00	−0.40	−0.20	−0.13	+0.26	−0.28	−0.04	−0.06		
4	.602	2,773	13.44	13.41	−.18	−.49	−.07	+.24	−.32	+.51	−.54		
5	.699	1,045	13.02	12.98	−.60	−.10	+.23	−.10	+.04	+.39	−.24		
6	.778	421	12.62	12.63	−1.05	−.14	+.11	−.33	+.42	+.07	−.31		
7	.845	225	12.35	12.36	−1.28	−1.04	−.18	−.96	+.60	+.24	−.62	−0.80	−1.41
8	.903	112	12.05	12.05	−1.45	−1.75	−.45	−.37	+.25	+.62	−.77	−.57	−.81
9	.954	43	11.63	11.55	−1.55	−1.55	−.29	−.10	+.18	+.72	−.44	−.33	−.64
10	1.000	10	11.00	11.10			−.25	−.62	−.25	+.51	−.02	−.12	−.56
11	1.041	4.29	10.63	10.72			−.02	−.42	+.06	+.36	−.02	+.04	−.44
12	1.079	2.14	10.33	10.33					−.03	+.27	+.62	+.25	−.26
13	1.114	1.44	10.16	10.15					−.15	+.45	+.70	−.24	−1.11
14	1.146	1.49	10.17	10.00					+.30	+.30	+.90	+.03	−.43
15	1.176	.77	9.89	9.82						+.18	+.88	−.01	−.40
16	1.204	.36	9.56	9.72							+.58	−.06	+.18
17	1.230	.37	9.57	9.61							+.87	−.31	−.53
18	1.255	.57	9.76	9.48							+1.22	−.53	
19	1.279	.37	9.57	9.35							+1.13	+.01	−.31
20	1.301	.17	9.23	9.27							+.73	+.15	+.15
21	1.322	.17	9.23	9.16							+.84		+.55
22	1.342	.16	9.20	9.08							+.92	+.07	+.34
23	1.362	.14	9.15	9.00									+1.11
24	1.380	.03	8.48	8.90									+.52
25	1.398	.09	8.95	8.83									+1.06
26	1.415	.11	9.04	8.75									+1.23
27	1.431	.14	9.15	8.67									+1.44
28	1.447	.14	9.15	8.60									+1.51
29	1.462			8.50									
30	1.477	.03	8.48	8.45									+.97
37	1.568	.03	8.48	8.00									+1.42
51	1.708	.01	8.00	7.35									+1.65

[1] Deviations were taken from the theoretical rather than observed values. The theoretical values were derived from the observed values by fitting straight lines to the points resulting from the plot of logarithm of numbers against logarithm of lengths in fig. 6.

[2] From 3 to 12 mm., inclusive, the average was of the first 7 cruises; from 13 to 51 mm., inclusive, it was of 9 cruises.

[3] 10 was added to the logarithm of each number in order to simplify notation in the case of decimal numbers.

There is, in addition, external evidence that the chosen series of homologies is correct and the alternate series incorrect.

The geographic distribution of successive stages needed to fit the alternate series would not be in harmony with any possible system of drifts. The 3- and 4-mm. larvae of cruise IV were off Long Island and the 6- to 8-mm. larvae of cruise V were mainly in the offing of the southern coast of New Jersey by the next cruise. To assume that these were homologous would require drifting at an average rate of 25 miles per day, which is far too fast for non-tidal currents in this area, comparing rather to such swift ocean currents as the Gulf Stream (Iselin, 1936, p. 43). On the other hand, the system of homologies indicated by the letters in figure 7 requires no fantastic assumptions as to drift. In fact, it will be shown below (p. 183) that the movements of larvae designated by this system of homologies follow a pattern closely and definitely related to wind-impelled drifts.

Furthermore, the growth rate of the larvae that would be indicated by the alternate series is not consistent with the lengths of the smallest post-planktonic stages. The range in size and the modal lengths of small post-planktonic mackerel taken in July and August of certain years have been indicated in figure 8. Unfortunately, the earliest available sample of such material in the 1932 measurements was drawn August 30, nearly 50 days after the latest tow net material. It lies close to the projected S–S and T–T lines of the chosen homologies and far from the projected line that would result from the alternative homologies. That this does not result by coincidence from altered growth rates intervening between cruise material and post-planktonic material is shown by the range and modal sizes from earlier dates in 1926